

TAXONOMY, EVOLUTION AND BIOSTRATIGRAPHICAL IMPORTANCE OF THE LLANDOVERY GRAPTOLITE *SPIROGRAPTUS*

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ABSTRACT. Four species are assigned to the Llandovery graptolite genus *Spirograptus*. *S. andrewsi* from the upper Aeronian, is the earliest representative and is recorded here for the first time outside Australia. *S. turriculatus* and *S. guerichi* sp. nov. occur in the lower Telychian. *S. guerichi* is distinguished from *S. turriculatus* by its lesser dorso-ventral width, rhabdosome apical angle and whorl diameter. The subspecies *S. turriculatus minor* is here considered a junior synonym of *S. turriculatus*. *S. minutus* is found only in the middle Telychian of Russia and is not described here. *Spirograptus* probably evolved from *Stimulograptus*. Evolution within *Spirograptus* involved initially increased curvature of the sicula, attainment of a greater dorso-ventral width and modification of the thecae. A new *Spirograptus guerichi* Biozone is erected to replace the *Spirograptus turriculatus minor* Biozone of some authors.

WHETHER there are one or two species of *Spirograptus* Gürich, 1908, in the lower Telychian (Upper Llandovery) has been debated since Bouček (1932) erected a subspecies, considered ancestral to *Spirograptus turriculatus* (Barrande, 1850), which he named *Monograptus turriculatus* mut. *minor* on the basis of its smaller size and its fewer spirals.

Some authors consider them synonyms (Rickards 1970; Hutt 1975; Lenz 1982; Melchin and Lenz 1986). This view was supported, but with the qualification that the greater number of small specimens occur in older strata, by Bjerreskov (1975) and Loydell (1991). Others (Sennikov 1976; Melchin 1989) recognized *S. turriculatus* and *S. t. minor* as distinct taxa and used *S. t. minor* as a biozonal index subspecies for the earliest part of the Telychian; the *S. t. minor* Biozone was succeeded by a *S. t. turriculatus* Biozone. Strachan (1971), Chen (1984), Fu and Song (1986), and Wang (1978) also recognized *minor* as a separate taxon, but did not use it as a biozonal index.

Here we demonstrate that there are two early Telychian spirograptid taxa (one of which is a new species), and that *S. turriculatus* and *S. t. minor* (as defined by Bouček 1932) are synonyms. The differences between *S. turriculatus* and our new species are illustrated both with material chemically isolated from limestone nodules, and with flattened specimens.

BIOSTRATIGRAPHICAL DIVISION OF THE EARLY TELYCHIAN

A variety of graptolite biozonal schemes has been used for the early Telychian. Some, however, use the same index species to denote different intervals: for example, the *turriculatus* Biozone of Bouček (1953) is equivalent to only the upper part of the *turriculatus* Biozone of Rickards (1976, 1989), and thus some confusion has arisen. (See, for example, Kříž 1991, text-fig. 1 who placed the base of the Telychian at the base of the *S. turriculatus* Biozone in Bohemia, at a level which does not correlate with the base of the Telychian elsewhere). Some of the biozonal schemes that have been employed for the lower Telychian are correlated in Text-figure 1.

SYSTEMATIC PALAEOONTOLOGY

The terminology used is mainly that of Bulman (1970). Thecal spacing is expressed in terms of a two theca repeat distance (2TRD; Howe 1983) with thecae per 10 mm quoted in brackets. Due to

LOYDELL 1992		LAPWORTH 1878 (Dob's Linn)	JONES 1921	RICKARDS 1976		BOUČEK 1953		MELCHIN 1989	
Biozone	Subzone	Biozone	Biozone	Biozone	Subzone	Biozone	Subzone	Biozone	
crispus			crispus	crispus		crispus		crispus	
turriculatus	carnicus		turriculatus	turriculatus		turriculatus	runcinatus (= storchi)	turriculatus	
	proteus						turriculatus		
	johnsonae								
utilis									
guerichi	renaudi		maximus			maximus	linnaei	hispanicus	minor
	gemmatus							palmeus	
	runcinatus								
halli		maximus	halli	sedgwickii		linnaei		minor	
sedgwickii	spinigerus	sedgwickii	sedgwickii				rastrum		

TEXT-FIG. 1. Correlation of graptolite biozonal and subzonal schemes for the upper Aeronian (*St. sedgwickii* and *St. halli* Biozones) and lower Telychian (*S. guerichi*-'*M.*' *crispus* Biozones) stages of the Llandovery. The *carnicus* subzone will be erected formally by J. Zalasiewicz (pers. comm.).

difficulties resulting from the rhabdosome's spiral curvature in measuring distance from the sicula in terms of number of thecae, measurements of dorso-ventral width are given for the mid-points of successive whorls instead of at specified thecae as is the normal practice. Dorso-ventral widths quoted are exclusive of thecal spines. The apical angle of the rhabdosome and the rhabdosome's diameter at specified whorls were measured only in specimens preserved with the axis of rhabdosome coiling approximately parallel to bedding, as was the number of whorls in 10 mm from the sicular aperture. Text-figure 2 illustrates the main features measured. The normal abbreviation for theca (th.) is used throughout the descriptions.

As there are many problems in taking measurements from spiral rhabdosomes oriented at a variety of different angles to bedding, figures quoted herein are approximate.

Synonymies include only the most important references; full synonymies of *S. guerichi* and *S. turriculatus* are given in Loydell (1992). Synonymies are annotated with the symbols listed by Matthews (1973).

Repositories of figured and cited material are abbreviated as follows: BGS, British Geological Survey, Keyworth; ROM, Royal Ontario Museum, Toronto; NIGP, Nanjing Institute of Geology and Palaeontology; NMP L, National Museum, Prague; PS, Štorch Collection, in the Geological Survey, Prague; UCWG, Institute of Earth Studies, University College of Wales, Aberystwyth.

Subfamily MONOGRAPTINAE Lapworth, 1873

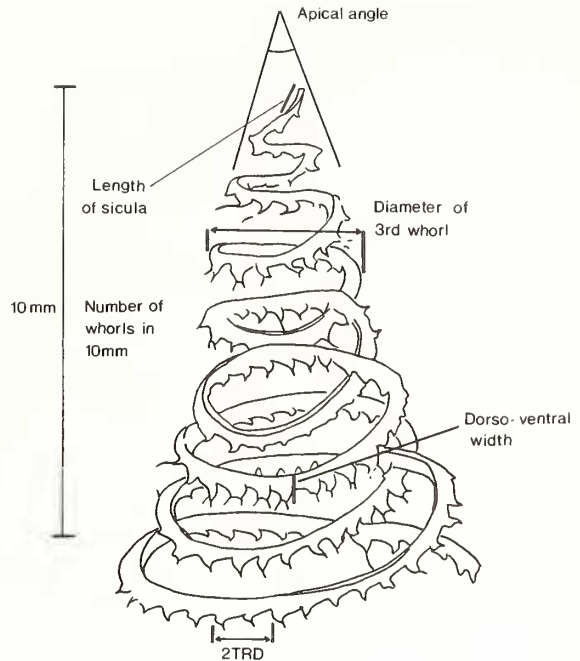
Genus SPIROGRAPTUS Gürich, 1908

(= *Tyrsograptus* Obut, 1949)

Type species. By subsequent designation of Bulman (1929, p. 182); *Graptolithus turriculatus* Barrande, 1850, p. 56, pl. 4, figs 7–11; from the Llandovery of Bohemia.

Diagnosis. Rhabdosome tightly trochispirally coiled; thecae hooked, in the manner of those of

TEXT-FIG. 2. Measurements taken from *Spirograptus* rhabdosomes. Dorso-ventral width was measured at the midpoint of each whorl. Whorl diameter was measured also at whorl five and the number of whorls in 5 mm from the sicular aperture was also recorded. 2TRD = two theca repeat distance (Howe 1983).



Stimulograptus Přibyl and Štorch, 1983, and bearing one or two apertural spines. Thecal apertures may be symmetrical, or asymmetrical resulting from the differential development of the apertural margin, but without significant torsion. Thecal overlap is negligible. Sicula is small (< 1.5 mm) and dorsally curved, in one species at least also exhibiting dextral torsion.

Remarks. Gürich's (1908, p. 34) original diagnosis for the genus ('Rhabdosom spiralg eingerollt, Zellen spitz endigen. Die Sicula ist an der Spitze der Spirale.') was emended by Mu (1955, p. 10) as follows: '*Monograpti* in which the rhabdosome is spiral, the thecae are hooked, usually with apertural spines.' Mu's (1955) diagnosis does not differ significantly from ours.

Přibyl (1945) included a large number of species within *Spirograptus*. These possess a variety of thecal forms, and belong to a number of different genera. Objections to Přibyl's (1945) usage of the genus (Mu 1955; Rickards *et al.* 1977) and incomplete knowledge of the thecal morphology of *S. turriculatus* resulted in a lack of wide acceptance of *Spirograptus*. However, with the description of chemically isolated specimens of *S. turriculatus* from the Canadian Arctic (Melchin and Lenz 1986), *Spirograptus* may now be more rigorously defined, and is of value in uniting a small number of closely related taxa.

Included within *Spirograptus*, as defined above, are *S. turriculatus* (Barrande, 1850), *S. guerichi* sp. nov., *S. andrewsi* (Sherwin, 1974) and *S. minimus* Obut and Morozova, 1988 (*in Obut et al.* 1988). The generic status of '*Monograptus*' *woodae* Haberfelner, 1931, is uncertain. The form of its tiny rhabdosome (which has a dorso-ventral width of 0.2 mm throughout its length, according to Haberfelner) suggests that it, too, may in the future be assigned to *Spirograptus*.

The thecal morphology of many species with spiral rhabdosomes previously assigned to *Spirograptus* is similar to that of '*Monograptus*' *planus* (Barrande, 1850) in that the apertural portion of the metathecae exhibits torsion so that apertures open onto the reverse side of the rhabdosome (see illustrations of chemically isolated specimens of '*M.*' *planus* in Loydell and Zhao 1990). Loydell (1992) erected a genus for this '*planus* group' which includes '*M.*' *denticulatus*

Törnquist, 1899, '*M.*' *involutus* Lapworth, 1876, '*M.*' *proteus* (Barrande, 1850), '*M.*' *spiraloides* (Příbyl, 1945) and probably '*M.*' *tullbergi* Bouček, 1931.

Other spiral taxa possess thecae which exhibit torsion only in part (mesially and distally) of the rhabdosome. In these cases, the whole of the theca is twisted, apertures are laterally expanded, and may bear spines. Species possessing such thecae should be assigned to *Oktavites* Levina, 1928, the type species of which, *Graptolithus spiralis* Geinitz, 1842, has recently been described from chemically isolated material from Canadian limestone nodules by Lenz and Melchin (1989). Loydell and Zhao (1990) illustrated the very similar thecal morphology of *Oktavites contortus* Perner, 1897, (described by Loydell and Zhao as *M.* aff. *M. spiralis*).

For several spirally curved species, thecal morphology is not yet known in sufficient detail for confident generic assignment to be made.

Spirograptus turriculatus (Barrande, 1850)

Plate 1, figs 2, 6; Text-figs 3A, 4A–G, 5

- v. * 1850 *Grapt. turriculatus* Barrande, p. 56, pl. 4, figs 7–11.
- p 1897 *Monograptus turriculatus*, Barr.; Perner, p. 15, pl. 12, figs 34, 36–38 (non 35 = *S. guerichi*).
- v. 1932 *Monograptus turriculatus* mut. *minor*, n. mut., Bouček, pp. 153, 155, figs 1c–d.
- . 1936 *Monograptus turriculatus* var. *fimbriatus*, Hundt, p. 29.
- v. 1945 *Spirograptus turriculatus turriculatus* (Barrande, 1850); Příbyl, p. 211, pl. 10, figs 1–2.
- v. 1945 *Spirograptus turriculatus minor* (Bouček, 1932); Příbyl, p. 213, text-fig. 3, pl. 20, figs 1–2 [copies of Bouček's 1932 figures].
- . 1971 *Monograptus* (*Spirogr.*) *turriculatus turriculatus* (Barr., 1850); Schauer, p. 74, pl. 30, figs 1–5; pl. 31, figs 11–13; pl. 45, figs 1–3.
- non 1974 *Monograptus turriculatus* (Barrande, 1850); Sherwin, p. 172, pl. 12, fig. 6 (= *S. guerichi*).
- p 1975 *Monograptus turriculatus* (Barrande, 1850); Bjerreskov, p. 70, pl. 10, fig. H.
- p 1982 *Monograptus turriculatus* (Barrande, 1850); Lenz, p. 118, figs 9N, 32E, 32G, 33B, 33C (non 32D, 33C = *S. guerichi*).
- v. 1986 *Monograptus turriculatus* (Barrande, 1850); Melchin and Lenz, p. 579, figs 1a–i.
- v. 1989 *Monograptus turriculatus turriculatus* (Barrande); Melchin, fig. 120.
- . 1990 *Spirograptus sinicus* Geh; Ge, p. 97, pl. 18, figs 1–7.
- vnon 1991 *Monograptus turriculatus* (Barrande, 1850); Loydell, p. 243, figs 7d, 8j, 10g, 11d, 12f (= *S. guerichi*).

Lectotype. Designated Příbyl 1945, p. 212; specimen NMP L 27597, figured Barrande 1850, pl. 4, fig. 10, from the Llandoverly of Litohlavý, Bohemia Pl. 1, fig. 6; Text-fig. 4F. Příbyl (1945), when selecting the lectotype, incorrectly stated its locality as Želkovice.

Material. Several hundred specimens from Litohlavý, Bohemia, including the type and figured material of Barrande (1850). Also Bouček's (1932) specimens of *Monograptus turriculatus minor* from Ratinka, Bohemia. The diagnosis and description below incorporate details (from Melchin and Lenz 1986) which are clearly visible

EXPLANATION OF PLATE I

Figs 1, 3, 5. *Spirograptus guerichi* sp. nov. 1, PŠ 358/1; lower *R. limnai* Biozone; Želkovice, Bohemia. 3, PŠ 360/1; upper *R. limnai* Biozone, Želkovice Formation; Hlásná Třeň, Bohemia. 5, PŠ 359/1, holotype; upper *R. limnai* Biozone, Želkovice Formation; Hlásná Třeň, Bohemia.

Figs 2, 6. *Spirograptus turriculatus* (Barrande). 2, NMP L 25043/245, lectotype of *Monograptus turriculatus minor* Bouček; '*M.*' *crispus* Biozone, Litohlavý Formation; Ratinka, Bohemia. 6, NMP L 27597, lectotype of *S. turriculatus*; *S. turriculatus* Biozone, Litohlavý Formation; Litohlavý, Bohemia.

Fig. 4. *Spirograptus andrewsi* (Sherwin). PŠ 513; upper *St. sedgwickii* Biozone, Želkovice Formation; Zdice, Bohemia.

All figures are $\times 5$.



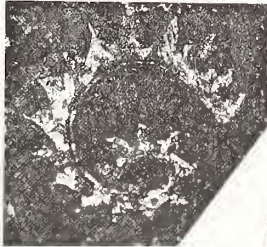
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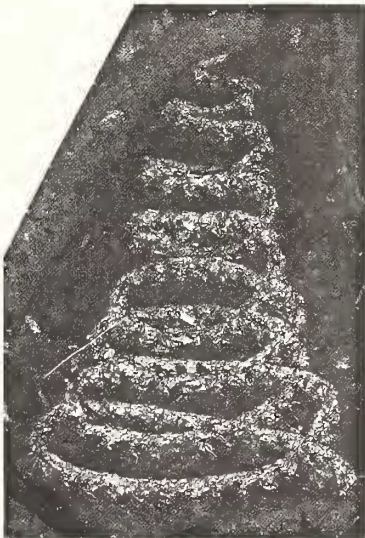
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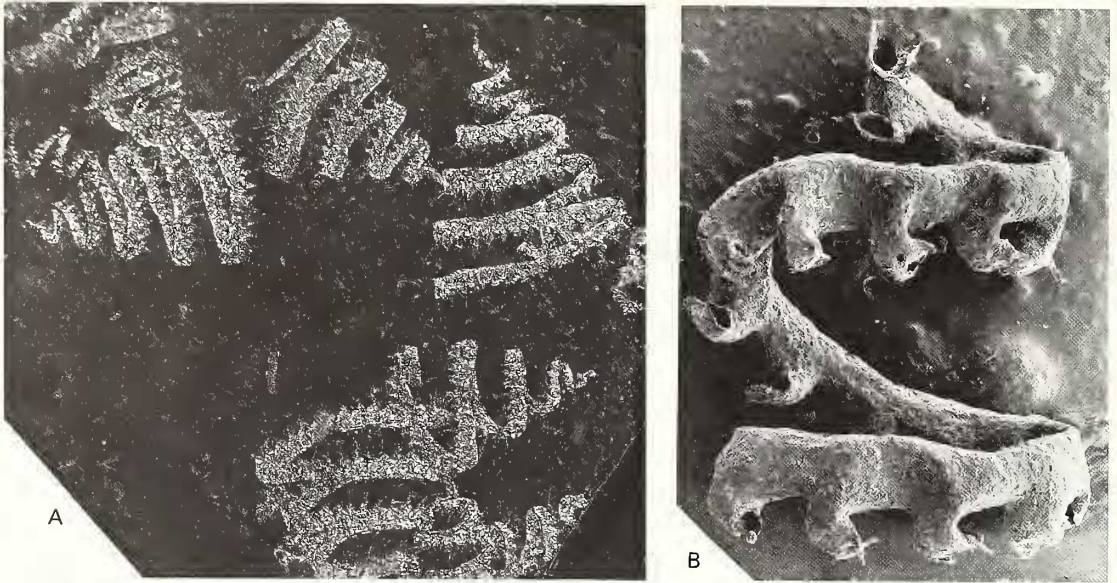
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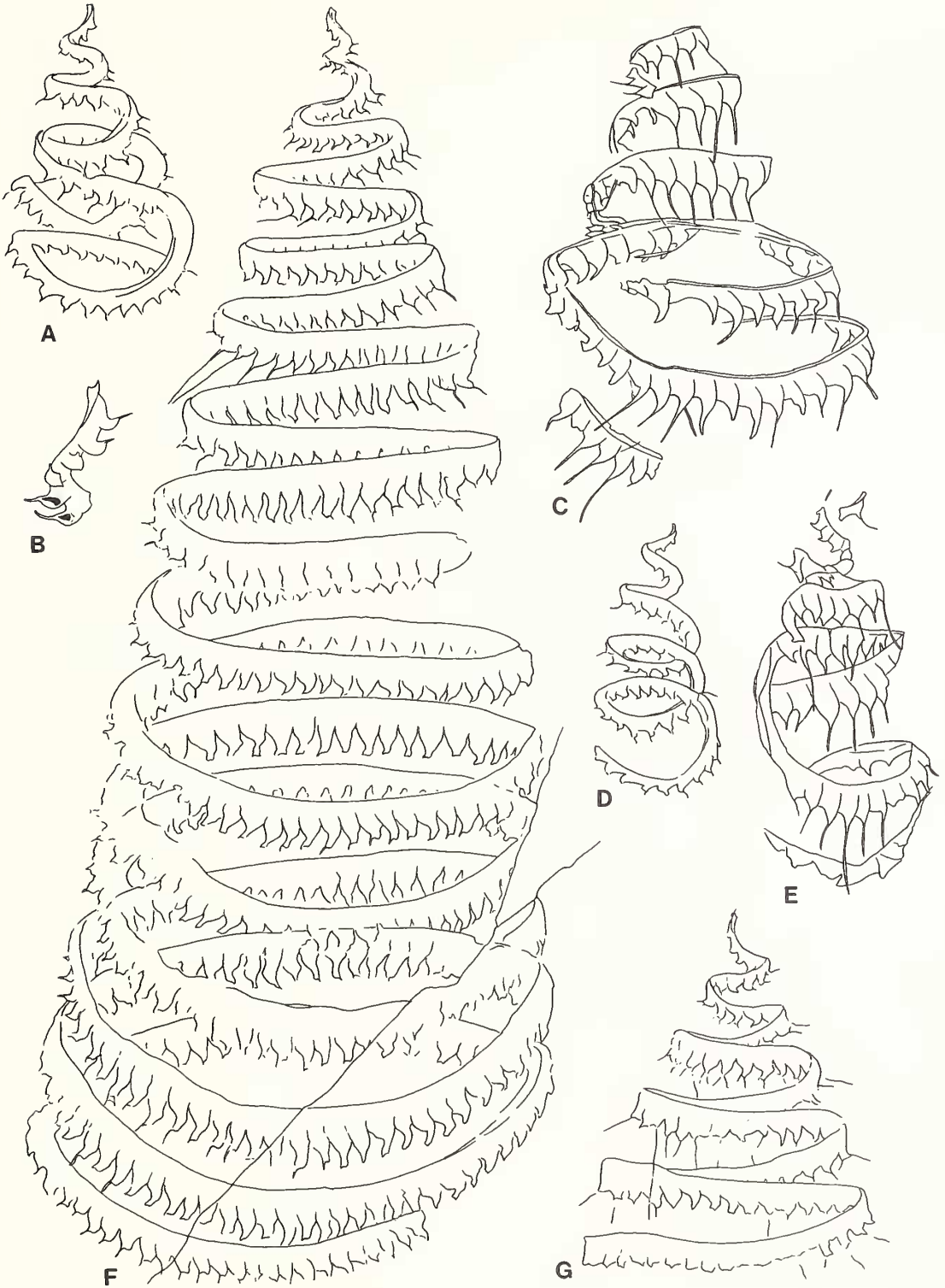
TEXT-FIG. 3. A, *Spirograptus turriculatus* (Barrande). PŠ 370/2; upper *S. turriculatus* Biozone, Litoahlavy Formation; Litoahlavy, Bohemia, $\times 2.9$. B, *Spirograptus guerichi* sp. nov. UCWG 267; isolated specimen, lacking proximal end; *S. guerichi* Biozone; Osmundsberget, Dalarna, Sweden, $\times 25$.

only in chemically isolated material. Other specimens examined are from western Wales and northwestern and Arctic Canada.

Diagnosis. Rhabdosome trochispirally coiled. Thecae hooked, with differential development of the apertural margin producing a tear-shaped aperture. Proximal thecae bear a single spine, directed to the obverse side of the rhabdosome. Distal thecae are less retroverted, and bear two spines. Dorsoventral width increases rapidly, such that by the fifth whorl it is nearly always greater than 1 mm. The diameter of the rhabdosome at the third whorl is usually within the range 4.7–5.8 mm (exceptionally 4.0 mm) and at the fifth whorl is 6.9–8.9 mm (exceptionally 6.2 mm). There are three to five whorls in 10 mm from the sicular aperture. The sicula is approximately 1 mm long, curved dorsally and has dextral torsion near its apex.

Description. The rhabdosome is trochispirally coiled through up to fourteen whorls in our material. The apical angle of the 'cone' formed by the rhabdosome generally lies between 40° and 50° . Thecae are without overlap, retroverted throughout, although less so distally. As a result of differential development of the apertural margin the thecal apertures are tear-shaped. Thecal axes are oriented parallel to that of rhabdosome growth.

TEXT-FIG. 4. *Spirograptus turriculatus* (Barrande). A, NMP L 25043/245, lectotype of *Monograptus turriculatus minor* Bouček; '*M.*' *crispus* Biozone, Litoahlavy Formation; Ratinka, Bohemia. B; chemically isolated proximal end showing one spine per theca (after Melchin and Lenz 1986). C, BGSDKL 1637; *Str. johnsonae* Subzone (*s. turriculatus* Biozone), Aberystwyth Grits Formation; locality A62 of Loydell (1992), western mid-Wales. D, NMP L 25043/244; obliquely preserved specimen; originally figured by Bouček (1932, fig. 1c) as *Monograptus turriculatus minor*. E, BGS DKL 2176; upper *St. utilis* Subzone (*S. turriculatus* Biozone), Aberystwyth Grits Formation; locality A50 of Loydell (1992), western mid-Wales. F, NMP L 27597, lectotype; *S. turriculatus* Biozone, Litoahlavy Formation; Litoahlavy, Bohemia. G, PŠ 370/2; *S. turriculatus* Biozone, Litoahlavy Formation; Litoahlavy, Bohemia. All figures $\times 5$, except B, which is $\times 10$.



Proximal thecae bear a single proximo-ventrally directed apertural spine on the apertural margin on the reverse side of the rhabdosome. Distal thecae bear two spines, that on the obverse side (inside of the spiral) being shorter than that on the reverse margin. In Bohemian specimens the earliest theca seen to possess paired spines is th5. Maximum lengths of spines in isolated material are 1.4 mm and 0.6 mm for those on the reverse and obverse apertural margins respectively. Spines on specimens preserved within the rock have been observed to be up to 2 mm in length. Measurements of dorso-ventral width at successive whorl mid-points in Bohemian and Welsh specimens are given in Table 1. Melchin and Lenz (1986) quote a dorso-ventral width at th1 of 0.5 mm, at th5 0.7 mm and, more distally, 1.3 mm. Maximum distal dorso-ventral width in flattened and low-relief specimens from Bohemia is 1.55 mm. At th2 in this material dorso-ventral width is 0.5–0.7 mm. More strongly diagenetically compressed Canadian material attains a maximum dorso-ventral width approaching 2 mm. 2TRD in isolated specimens is 1 mm proximally, and 1.5 mm distally. In Bohemian material, distal 2TRD is 1.1–1.2 mm, 0.9–1.3 mm being the range observed in Welsh specimens. The sicula, 0.8–1.0 mm in length, is dorsally curved and undergoes slight dextral torsion near its apex, which reaches to the top of th2.

TABLE 1. Measurements of dorso-ventral width (DVW) at the mid-points of successive whorls of Welsh and Bohemian specimens of *Spirograptus turriculatus* (Barrande, 1850).

Whorl...	2	3	4	5	6	7	8
DVW (Wales) (<i>n</i> = 28)	0.7–1.0	0.85–1.25	1.0–1.3	1.15–1.4	1.2–1.3		
DVW (Bohemia) (<i>n</i> = 21)	0.5–0.85	0.75–1.1	0.85–1.2	0.95–1.25	0.95–1.35	1.0–1.4	1.0–1.5

Remarks. The differences between *S. turriculatus* and other spirograptids are summarized in Table 3. In fully developed rhabdosomes preserved with the rhabdosome coiling axis parallel to bedding distinguishing specimens of *S. turriculatus* from other spirograptids is not difficult.

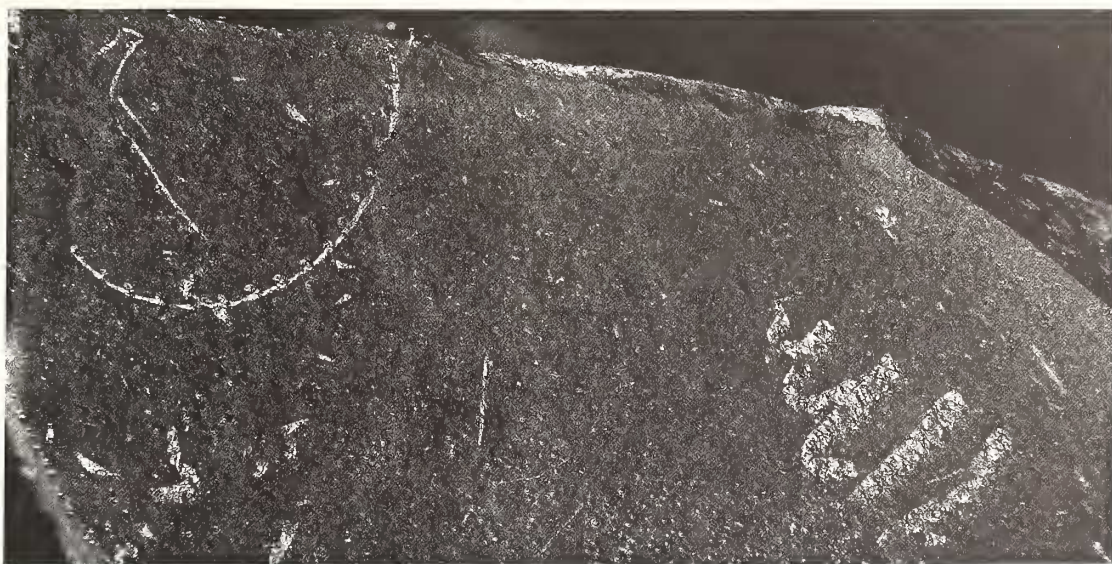
Schauer (1971) distinguished two 'Formgruppen', A and B, of *S. turriculatus* on the basis of average number of whorls and the position of the longest thecal spines within the rhabdosome. 'Formgruppe A' is characterized by 7.5 to 8 whorls and particularly long thecal spines proximally and mesially. 'Formgruppe B', confined stratigraphically to the *crispus* Biozone, consists of, on average, 8–10 whorls, with spines particularly prominent distally.

Hutt (1975, p. 112) noted bifurcating spines on some specimens of *S. turriculatus* from the English Lake District. This phenomenon might account for earlier suggestions (Bulman and Rickards 1970) of each theca possessing more than two apertural spines. Some Bohemian specimens also appear to possess more than two spines on distal thecae.

Hundt's (1936) subspecies *fimbriatus* was erected in the erroneous belief that the thecae of *S. turriculatus* lack spines. The supposed distinguishing feature of *fimbriatus* was the presence of 'Härchen' (hairs). Přibyl (1945) placed *fimbriatus* in synonymy with *turriculatus*.

Bouček's (1932) figures of the subspecies *minor* were copied by Přibyl (1945). These figures are misleading in that they suggest that the specimens are narrower than they really are (compare Bouček's figures with Text-figures 4A and 4D herein). The lectotype of *S. t. minor*, selected by Přibyl (1945), is preserved somewhat obliquely to bedding (note the position on the virgula on final whorl; Text-fig. 4A) and thus dorso-ventral width cannot be measured accurately. Comparison of Text-figure 4A with 4F (lectotype of *S. turriculatus*) indicates that *S. turriculatus* and *S. turriculatus minor* are conspecific; however, comparison of Text-figure 4A with Text-figures 6C–H illustrates the larger size of *minor* as compared to *guerichi*. The other specimen figured by Bouček (1932, fig. 1c; Text-fig. 4D) is preserved even more obliquely to bedding than the lectotype, and would be very difficult in isolation to assign with confidence to either *S. guerichi* or *S. turriculatus*. However, the torsion of the sicula, characteristic of *S. turriculatus*, is visible in this specimen.

On the reverse side of the slab bearing the lectotype of *S. t. minor* is a specimen of '*Monograptus*'



TEXT-FIG. 5. Reverse side of slab (NMP L 25043/245) bearing lectotype of *Monograptus turriculatus minor* on obverse. '*Monograptus*' *crispus* Lapworth, 1876 is at top left; *Spirograptus turriculatus* (Barrande, 1850) is at bottom right; Litohlavý Formation; Ratinka, Bohemia, $\times 5$.

crispus Lapworth, 1876, (Text-fig. 5). This species not found in strata yielding *S. guerichi*, but occurs with *S. turriculatus* in the '*M.*' *crispus* Biozone. There is no longer an exposure at the type locality for *S. t. minor* at Ratinka, Bohemia.

Spirograptus guerichi sp. nov.

Plate 1, figs 1, 3, 5; Plate 2, figs 1-6, 8-10; Text-figs 3B, 6C-H

- p 1897 *Monograptus turriculatus* Barr.; Perner, p. 15, pl. 12, fig. 35 (non 34, 36-38 = *S. turriculatus*).
 . 1971 *Monograptus turriculatus minor* Bouček, 1932; Schauer, p. 74, pl. 30, figs 7-8; pl. 31, figs 7-9.
 . 1974 *Monograptus turriculatus* (Barrande, 1850); Sherwin, p. 172, pl. 12, fig. 6.
 p 1975 *Monograptus turriculatus* (Barrande, 1850); Bjerreskov, p. 70, (non pl. 10, fig. H = *S. turriculatus*).
 ? 1976 *Spirograptus minor* (Bouček, 1932); Sennikov, p. 194, pl. 13, figs 5-7.
 ? 1978 *Spirograptus minor* (Bouček); Wang, p. 311, pl. 1, fig. 7.
 p 1982 *Monograptus turriculatus* (Barrande, 1850); Lenz, p. 118, figs 32D, 33C (non figs 9N, 32E, 32G, 33A-B = *S. turriculatus*).
 v. 1984 *Spirograptus turriculatus* (Barrande); Chen, p. 70, pl. 15, figs 9-10; pl. 16, figs 1-2.
 v. 1984 *Spirograptus minor* (Bouček); Chen, p. 71, pl. 16, figs 3-4, 7 (? 12).
 1986 *Spirograptus turriculatus minor* (Bouček); Fu and Song, p. 121, pl. 12, figs 11-14.
 v. 1989 *Monograptus turriculatus minor* Bouček; Melchin, fig. 11M.
 v. 1991 *Monograptus turriculatus* (Barrande, 1850); Loydell, figs 7d, 8j, 10g, 11d, 12f.

Derivation of name. After G. Gürich, author of the genus *Spirograptus*.

Holotype. Specimen no. PŠ 359/1; from the uppermost part of the Želkovice Formation at Hlásná Třeboň, Bohemia; Llandovery, upper *Rastrites linnaei* Biozone (Pl. 1, fig. 5; Text-fig. 6D).

Material. Several hundred chemically isolated specimens from limestone nodules from Osmundsberget,

Dalarna, Sweden (nodules from within 4 m above the unconformable contact between the Llandovery and the Upper Ordovician Boda Limestone; from sections on both sides of quarry at northern end of main quarry, 4.5 km north of Boda Church, Siljan District [UTM Grid Reference WH 1095 6870]); these are almost exclusively proximal fragments, representing the first one to three whorls. More than one hundred low relief (pyrite) specimens from the early Telychian sequences of Hlásná Třebeň, and Želkovice (Bohemia). Several hundred specimens from western mid-Wales (see Loydell in press) and from northwestern and Arctic Canada.

Diagnosis. Tightly trochispirally coiled rhabdosome bears hooked thecae, each furnished with two apertural spines. Maximum dorso-ventral width (excluding spines) averages 1 mm (maximum is 0.8 mm in Bohemian material). In specimens compressed with the axis of coiling approximately parallel to bedding, rhabdosome diameter at whorl 3 usually falls within the range 3.4–4.3 mm and at whorl 5 is 5.0–5.7 mm. In 10 mm from the sicular aperture there are 6–7 whorls. Sicular dorsally curved, 0.8–1.15 mm in length.

Description. The rhabdosome is trochispirally coiled. Specimens exhibiting more than seven whorls are rare, eight whorls being the maximum recorded. The apical angle of the 'cone' formed by the rhabdosome usually lies in the range 30–40°, but may be greater and, very rarely, exceeds 50°. In Bohemian material the diameter of the rhabdosome at the third whorl usually falls within the range 3.4–4.3 mm (maximum 4.8 mm) and at the fifth whorl is 5.0–5.7 mm. There are usually 6–7 whorls in 10 mm from the sicular aperture. The thecae are hooked, with simple symmetrical apertures. Distal to th₂, the thecae show slight torsion so that the apertures are directed to the reverse side of the rhabdosome (i.e. inwards, towards the centre of the spiral). Th₁ exhibits no such torsion. The periderm of the dorsal wall of the metathecae is very thin and is rarely preserved (in isolated specimens, Plate 2, figs 1 and 5). Thecal apertures are furnished at their lateral margins by a pair of ventro-laterally directed spines, up to 0.8 mm in length (invariably broken on isolated specimens). In isolated specimens dorso-ventral width is 0.42–0.47 mm at th₁, with a maximum distal value of 0.7 mm. Flattened and low relief specimens from Bohemia have a dorso-ventral width of c. 0.4 mm at th₂ and a maximum distal dorso-ventral width of 0.8 mm. Welsh specimens attain a maximum dorso-ventral width of 1.0 mm, whilst Arctic Canadian specimens (the most diagenetically flattened in our collections) attain a maximum dorso-ventral width of 1.2 mm. Measurements of dorso-ventral width at successive whorl mid-points for Welsh and Bohemian specimens are given in Table 2. Thecal overlap is negligible. Thecae are very closely spaced. 2TRD in Welsh specimens is 0.8–1.2 mm (25–17 thecae in 10 mm) at the mid-point of whorl 2 and increases to 1.0–1.3 mm (20–15 thecae in 10 mm) distally. The sicular is dorsally curved, 0.8–1.15 mm in length. Its apex reaches to from just below the base of th₂ to just below the base of th₃.

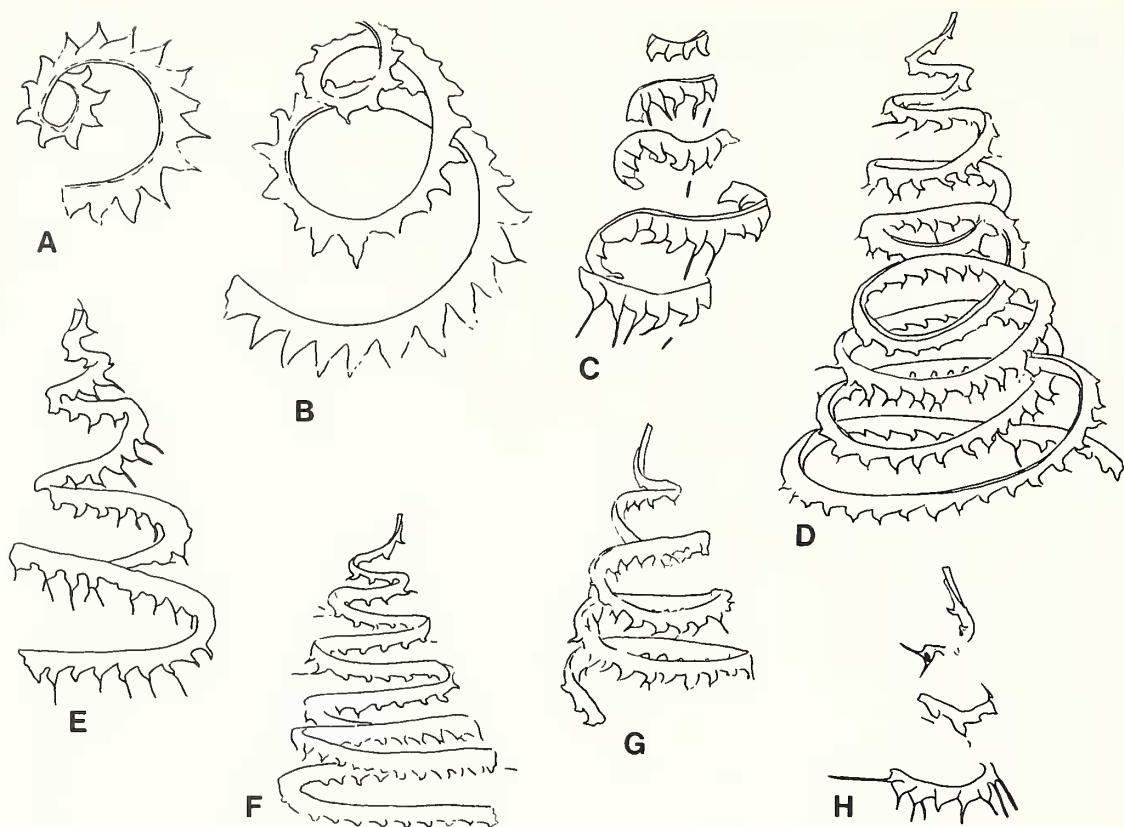
Remarks. The differences between *S. guerichi*, *S. turriculatus* and the other spirograptid species are summarized in Table 3. *S. andrewsi* (Sherwin, 1974) differs primarily from *S. guerichi* in its much greater apical angle (giving the rhabdosome a very low trochispiral form) which results in specimens preserved with the coiling axis perpendicular to bedding being by far the most commonly encountered. *S. minimus* has a maximum dorso-ventral width of only 0.7 mm and has narrower prothecal bases than *S. guerichi*. As the extreme of the range of variation in apical angle values in *S. guerichi* overlaps with the commonest apical angle observed in *S. turriculatus*, this on its own is

EXPLANATION OF PLATE 2

Figs 1–6, 8–10. *Spirograptus guerichi* sp. nov.; chemically isolated specimens; *S. guerichi* Biozone; Osmundsberget, Dalarna, Sweden. 1, UCWG 934C; part of first whorl; note poor preservation/absence of dorsal wall; all but one spines have been broken off, × 50. 2, UCWG 934A; thecal aperture and one of the apertural spines of th₃, × 150. 3, UCWG 953D; looking down upon sicular aperture and aperture of th₁, × 50. 4, UCWG 945I; dorsally curved sicular and protheca of th₁, × 50. 5, UCWG 953E; proximal end, note paired spines on th₁, × 50. 6, UCWG 945J; dorsally curved sicular and protheca of th₁, × 50. 8, UCWG 934C; × 30. 9, UCWG 934D; proximal end, note paired spines on th₂, × 50. 10, UCWG 934B; × 30.
Fig. 7. *Stimulograptus halli* (Barrande), UCWG 937F; chemically isolated proximal end; *S. guerichi* Biozone; Osmundsberget, Dalarna, Sweden, × 25.



LOYDELL *et al.*, *Spirograptus*, *Stimulograptus*



TEXT-FIG. 6. A–B, *Spirograptus andrewsi* (Sherwin). Upper *St. sedgwickii* Biozone, Želkovice Formation; Zdice, Bohemia; A, PŠ 513a. B, PŠ 513b. C–H, *Spirograptus guerichi* sp. nov. C, BGS DKL 1981; Cwmsymlog Formation, 'M.' *gemmatus* Subzone (*S. guerichi* Biozone); locality C1 of Loydell (1992), western mid-Wales. D, PŠ 359/1, holotype; Želkovice Formation, upper *R. linnaei* Biozone; Hlásná Třeboň, Bohemia. E, ROM 46011; Cape Phillips Formation; Huff Ridge, Ellesmere Island, Canada. F, PŠ 360/1; Želkovice Formation, upper *R. linnaei* Biozone; Hlásná Třeboň, Bohemia. G, PŠ 358/1; Želkovice Formation, lower *R. linnaei* Biozone; Želkovice, Bohemia. H, BGS DKL 819; Aberystwyth Grits Formation, lower *St. utilis* Subzone (*S. guerichi* Biozone); locality A16 of Loydell (1992), western mid-Wales. All figures are $\times 5$.

TABLE 2. Measurements of dorso-ventral width (DVW) at the mid-points of successive whorls of Welsh and Bohemian specimens of *Spirograptus guerichi* sp. nov.

Whorl...	2	3	4	5	6	7
DVW (Wales) (<i>n</i> = 25)	0.5–0.7	0.58–0.85	0.6–0.9	0.85–0.9	0.75	
DVW (Bohemia) (<i>n</i> = 31)	0.45–0.6	0.45–0.7	0.55–0.7	0.6–0.75	0.65–0.8	0.7–0.8

not an infallible basis for distinguishing the two taxa. The greater dorso-ventral width, and whorl diameter of *S. turriculatus* are the most useful of the features listed in Table 3 for separating this species from *S. guerichi*.

TABLE 3. Comparison of *Spirograptus* species (w. = whorl).

species feature	andrewsi	guerichi	turriculatus	minimus
Sicula: shape	Slightly dorsally curved	Dorsally curved No torsion	Dorsally curved Dextral torsion near apex	Not known
length	1.2-1.4	0.8-1.15	0.8-1.0	
Thecal apertures	Symmetrical (in Sherwin's 1974 reconstruction)	Symmetrical	Asymmetrical (tear-shaped)	Not known
Thecal spines	Probably single	Paired	Prox. single Dist. paired (and bifurcating?)	Number not known
length (max.)	1.3	0.8	2.0	1.5
Max. no. of whorls	3	8	16	4
Apical angle	Higher than turriculatus	30-40°	40-50°	c. 40°
Dorso-ventral width	w.3 1.1-1.2 w.5 0.95 max. 1.1-1.2 (Aust.) (Bohemia)	0.45-0.85 0.6-0.9 0.8-1.2	0.75-1.25 0.95-1.4 1.5-2.0	c.0.5 0.7
Whorl diameter	w.3 w.5	3.4-4.3 (exceptionally 4.8) 5.0-5.7	4.7-5.8 (exceptionally 4.0) 6.9-8.9 (exceptionally 6.2)	3.3-3.5
No. of whorls	in 5mm 10mm	3-5 6-7	2-3 3-4	3
Other features				Prothecae are narrower at base than in guerichi

The differences between *S. guerichi* and Bouček's (1932) specimens of *S. turriculatus minor* have been discussed above under *S. turriculatus*. In general, specimens referred to *S. t. minor* by non-Bohemian authors are *S. guerichi* (see synonymy list above and Loydell 1992).

Příbyl (1945) and Schauer (1971) used the number of whorls comprising the rhabdosome to distinguish between *S. turriculatus* and *S. guerichi* (which they identified as the subspecies *minor*). Specimens of *S. turriculatus* may possess up to sixteen whorls (according to Obut *et al.* 1988), with fourteen the maximum observed in Bohemian material. Eight is the maximum number recorded in *S. guerichi*. This does not allow growth stages possessing fewer whorls to be distinguished.

Considerable caution should be exercised when attempting to identify to specific level specimens which are preserved obliquely to bedding, short proximal fragments, and also tectonically distorted specimens. Schauer (1971) illustrated the dramatic effects of tectonic distortion on *S. turriculatus*, recognizing 'tektonische Langformen', 'tektonische Kurzformen' and 'tektonischen Schrägformen', depending upon the orientation of the rhabdosome to the direction of principal stress.

That Hutt *et al.* (1971) did not encounter specimens which now would be attributable to *S. guerichi* in their study of the Osmundberget fauna is surprising as this species was common in the nodules processed for this present work.

Biostratigraphically, *S. guerichi* is restricted to the earliest Telychian (Text-fig. 7), making its last appearance in the lowest part of the *S. turriculatus* Biozone (upper *Stimulograptus utilis* Subzone of Loydell 1991). Loydell (in press) noted that the species appears to be cosmopolitan, and not geographically restricted in its distribution as was suggested by Melchin (1989).

Spirograptus andrewsi (Sherwin, 1974)

Plate 1, fig. 4; Text-fig. 6A–B

* 1974 *Monograptus andrewsi* sp. nov., Sherwin, p. 170, pl. 10, figs 5–6; pl. 11, fig. 11; pl. 12, fig. 8; text-figs 3a–c.

Holotype. By original designation, the specimen illustrated by Sherwin 1974, pl. 11, fig. 11, from the Llandovery of the Forbes District, New South Wales, Australia.

Material. Approximately thirty flattened, mostly incomplete specimens from the upper part of the *Stimulograptus sedgwickii* Biozone of Zadní Třebañ, Zdice ('Colonie Lapworth'), and Želkovice, Bohemia. This level in Bohemia possibly correlates with the *Stimulograptus halli* Biozone of Britain (see Loydell 1991).

Diagnosis. Rhabdosome forms a very low trochispiral. Thecae hooked and spinose, without overlap. Proximal dorso-ventral width 0.5–0.6 mm, distally 0.55–0.95 mm in Australian specimens, 1.1–1.2 mm in Bohemian specimens. Sicula 1.2–1.4 mm long, very gently dorsally curved, its apex reaching half way up th2.

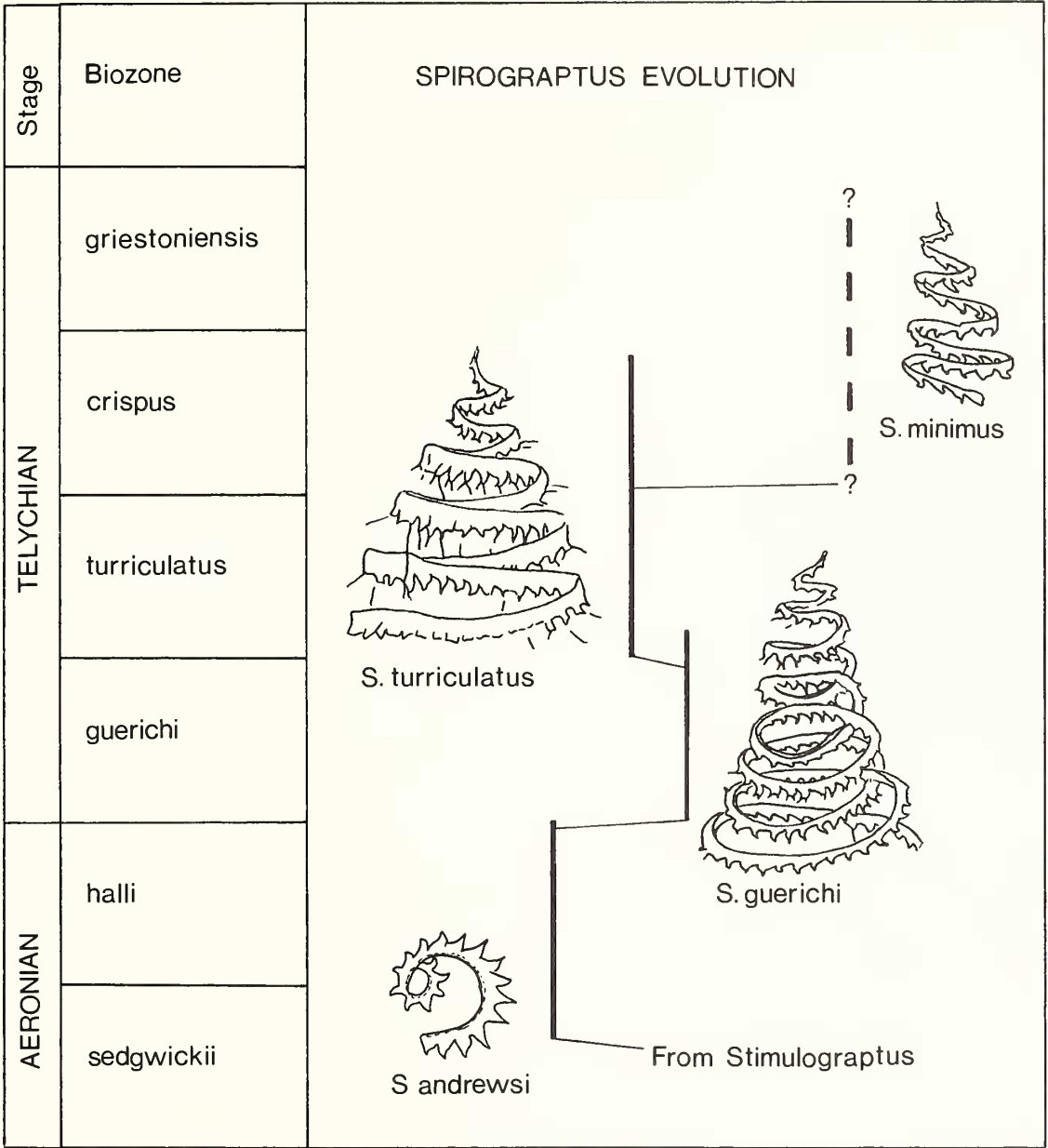
Description. In the Bohemian material, the rhabdosome is in the form of a very low trochispiral, with a maximum of three whorls developed. The maximum diameter of the last whorl is 8 mm. The sicula and earliest thecae have not been seen. The thecae are triangular, without overlap. The ventral thecal wall is inclined at c. 45° to the rhabdosome axis. The dorsal wall is nearly perpendicular to this axis. Stout thecal apertural spines are up to 0.45 mm in length but many are broken. There appears to be only one spine per theca. Proximal dorso-ventral width is 0.6–0.75 mm increasing to a maximum of 1.1–1.2 mm distally. 2TRD is 1.4–1.95 mm at the mid-point of whorl two.

Remarks. The form of the rhabdosome and the very gentle sicular curvature are useful in distinguishing this species from *S. turriculatus* and *S. guerichi* (see Table 3). Short fragments could prove impossible to distinguish, however.

Sherwin's (1974) specimens of *S. andrewsi* were collected from strata older than those yielding *S. guerichi* (described as *Monograptus turriculatus* by Sherwin), a situation which parallels that in Bohemia. Sherwin was unsure as to whether the thecae of *S. andrewsi* bear one or two spines.

PHYLOGENY

The close similarity between the thecal morphology of *S. turriculatus* and that of *Monograptus sedgwickii* (Portlock, 1843), a species now assigned to *Stimulograptus* Přibyl and Štorch, 1983, was noted by Elles and Wood (1913). Plate 2, figure 7 illustrates the proximal end of another



TEXT-FIG. 7. Evolution within *Spirograptus*.

stimulograptid, *Stimulograptus halli* (Barrande, 1850), for comparison with that of *S. guerichi*, which is strikingly similar (Pl. 2, fig. 5) except for its curvature. Melchin and Lenz (1986) proposed that *St. sedgwickii* was directly ancestral to *S. turriculatus* and indeed it seems certain that the spirograptids evolved from a stimulograptid ancestor by introduction of a spiral rhabdosome morphology accompanied by curvature of the sicula.

Within *Spirograptus*, early evolution involved increasing curvature of the sicula, changes in thecal

morphology, more rapid attainment of a greater dorso-ventral width and also an increase in the overall number of whorls (Text-fig. 7). The stratigraphically youngest representative of the genus, *Sp. minimus* Obut and Morozova, 1988 (in Obut *et al.* 1988) is also the most diminutive, however.

A REVISED BIOZONAL SCHEME FOR THE EARLY TELYCHIAN

With *Monograptus turriculatus minor* proving to be a junior synonym of *Spirograptus turriculatus*, the *minor* Biozone of authors being based upon *S. guerichi*, and *S. turriculatus sensu stricto* absent from strata currently assigned to the earliest Telychian (the lower part of the *turriculatus* Biozone (Rickards 1989)) a revision of early Telychian biostratigraphy is necessary.

The *S. guerichi* Biozone is here erected for the interval from the first appearance of *S. guerichi* to the first appearance of *S. turriculatus*, the end of the *turriculatus* Biozone being marked by the first appearance of '*Monograptus*' *crispus* Lapworth, 1876. *S. guerichi* is virtually confined to its biozone (Text-fig. 7), whilst *S. turriculatus* ranges high into the *crispus* Biozone.

With regard to the base of the Telychian Stage, the only identifiable graptolite recovered from the Telychian of the Llandovery Series of the Llandovery area (Cocks *et al.* 1984) appears to be lost. If this specimen is *Paradiversograptus runcinatus* (Lapworth, 1876), as identified by Cocks *et al.* (1984), then this would probably mean that the base of the Telychian, as formally defined in Bassett (1985), may coincide roughly with the base of the *S. guerichi* Biozone. *Pa. runcinatus* has its acme in the lower part of the *S. guerichi* Biozone (Bjerreskov 1975; Loydell 1991).

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